Morphological Variation in Turtles of the Genus *Pseudemys* (Testudines: Emydidae) From Central Atlantic Drainages

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ABSTRACT.— Thirty morphometric and 15 qualitative characters were analyzed to compare *Pseudemys rubriventris*, *P. floridana floridana*, and *P. concinna concinna* in the eastern United States. Taxonomic characters that have been employed to define these species are reexamined. Principal components and discriminant analyses indicate that *P. rubriventris* is morphologically distinct from the other two *Pseudemys*. Several additional useful taxonomic characters were found, but some character convergence or hybridization between *P. rubriventris* and congeners was detected. No morphometric divergence was found between *P. f. floridana* and *P. c. concinna*, and only markings appear to separate the two forms. As reported in previous works, *P. floridana* inhabits the coastal plain and *P. concinna* inhabits the piedmont. Populations occurring in a relatively broad area overlapping the Fall Line of North Carolina have morphological character states that are variable and somewhat intermediate between these two species.

Cooter and redbelly turtles are aquatic species of emydids that inhabit the eastern and south-central United States. They are relatively large (up to 420 mm carapace length) basking species with striped head markings and primarily herbivorous feeding habits. Following Seidel and Smith (1986) and Ward (1984), current classification places these turtles in the genus *Pseudemys*, separate from sliders (*Trachemys*) and painted turtles (*Chrysemys*) (Collins 1990, Ernst and Barbour 1989, King and Burke 1989). The genus *Pseudemys* includes three redbelly species [*P. alabamensis* Baur, *P. nelsoni* Carr, *P. rubriventris* (LeConte)] and three cooter species [*P. concinna* (LeConte), *P. floridana* (LeConte), *P. texana* Baur].

Taxonomic relationships in the genus *Pseudemys* are problematic as indicated by an extensive history of species-subspecies revisions (see Smith and Smith 1980 for a review). Frequently, in areas of sympatry, evidence of hybridization has been reported. Some populations with intermediate (hybrid?) characters are geographically broad, which suggests subspecific relationships. These interactions have been examined in Florida (Crenshaw 1955) and Louisiana (Fahey 1980). Part of the problem has arisen from the absence of clearly defined quantifiable characters that separate species of *Pseudemys*. Another problem has been the relatively small number of specimens examined, especially from northern populations. The most recent taxonomic analysis with species diagnoses of *Pseudemys* relies heavily on cranial musculature and osteology (Ward 1984). Unfortunately those characters are of little use in field identification or in evaluation of fluid-preserved museum material.

In spite of the taxonomic attention *Pseudemys* has received, we have found that species of the eastern United States (Atlantic slope) remain very difficult to identify using available diagnostic characters. Nearly all key characteristics are qualitative and based on highly variable markings and shell shapes. The problem of identification is especially acute in the coastal plain of Virginia and North Carolina where the ranges of *P. rubriventris*, *P. concinna concinna*, and *P. floridana floridana* overlap or come in contact. In that area Crenshaw (1965) noted putative hybridization between *P. rubriventris* and *P. floridana*, and Martof et al. (1980) reported frequent hybridization between *P. concinna* and *P. floridana*, commenting that some specimens defy classification at the species level. The objectives of the present study were: (1) to identify external characters that more reliably distinguish these turtles in Virginia and North Carolina, (2) to identify individual turtles from this region that appear to be morphologically intermediate, and (3) to characterize patterns of *Pseudemys* distribution in the central Atlantic coastal plain.

METHODS

For morphometric analysis, 76 fluid-preserved *P. rubriventris* (New Jersey, Pennsylvania, West Virginia, Virginia, North Carolina), 57 *P. c. concinna* (Virginia, North Carolina, South Carolina), and 59 *P. f. floridana* (Virginia, North Carolina, South Carolina) were analyzed (Fig. 1). Specimens included freshly collected individuals with typical coloration as well as museum specimens (see Specimens Examined). Abbreviations for museums follow Leviton et al. (1985), and MES = reference collection of the senior author. All turtles were tentatively identified to species a priori using traditional qualitative characters (mostly markings, see Table 1) that have been applied to distinguish *P. concinna*, *P. floridana*, and *P. rubriventris* (Ernst and Barbour 1972, 1989, Conant and Collins 1991). If assignment was questionable, that

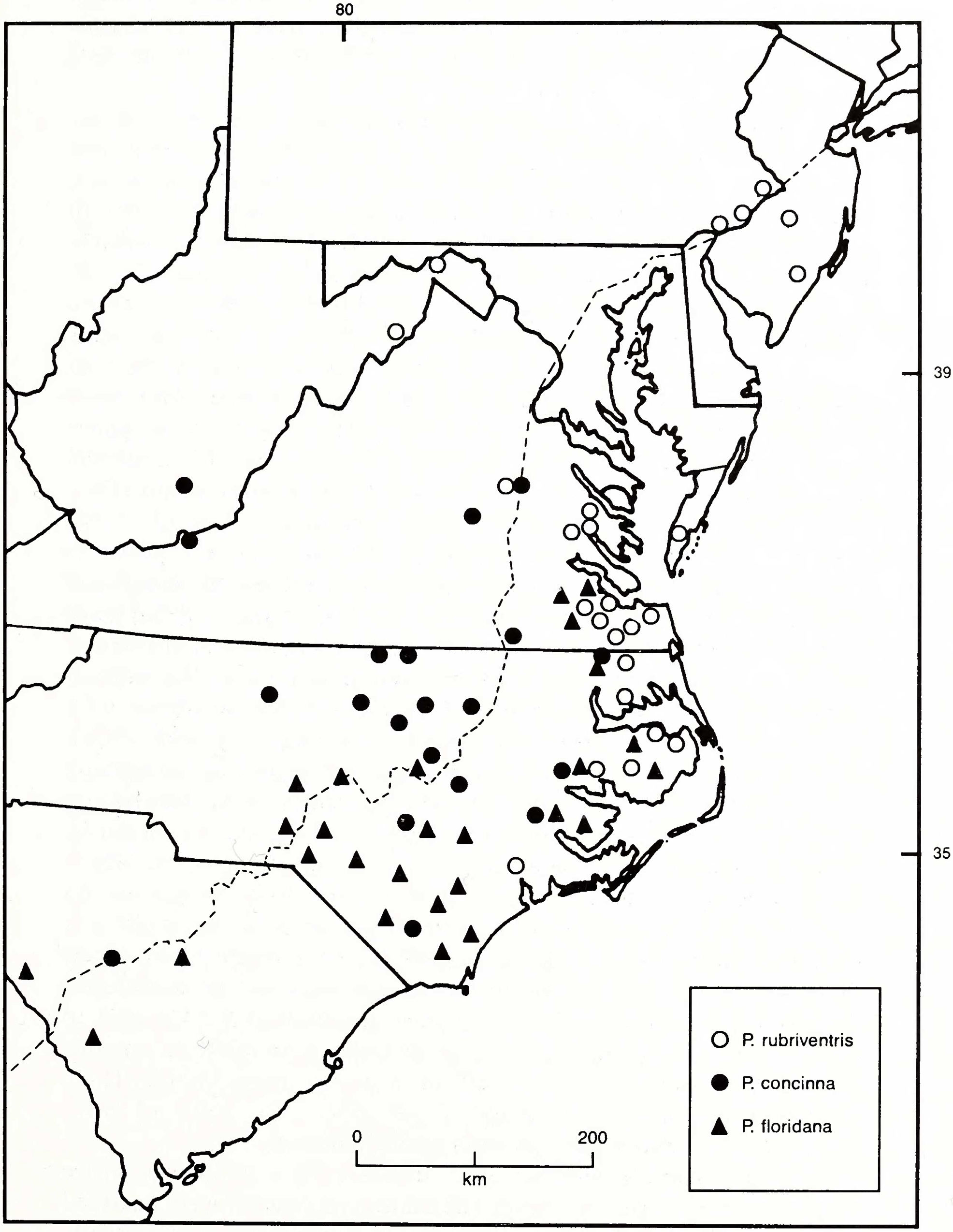

Fig. 1. Localities of adult *Pseudemys* specimens examined for morphometric analysis. The Fall Line is indicated by a broken line.

was noted. These identifications often agreed with specific assignments in museum collections, although many specimens from coastal Virginia and North Carolina are catalogued as "*Pseudemys* sp?" or only tentatively assigned to species.

Character states for 15 qualitative characters were recorded for each turtle. Twenty-six shell characters were measured on each specimen with calipers (Helios) or a goniometer (Jamar). Two head-neck stripes, head width, and maxillary cusp length were also measured. These 30 measurements (Fig. 2-7) included all quantifiable external characters that have been used to diagnose *P. concinna*, *P. floridana*, or *P. rubriventris*, as well as additional characters suspected to have taxonomic value: carapace length along midline (CL), carapace width at sulcus between marginals V-VI (CW), carapace width at sulcus between marginals VII-VIII (SW), plastron length along midline (PL), shell height at sulcus between vertebrals II-III (CH), shell height at sulcus between vertebrals III-IV (SH), cervical scute dorsal length (CS), cervical scute dorsal posterior width (CD), cervical scute ventral length (CU), cervical scute ventral posterior width (CV), marginal XII length (MH), marginal XII anterior dorsal width (MA), marginal XII posterior (ventral) width (MP), lateral angle of carapace formed by dorsal and ventral surfaces of marginal VI (SA), posterior angle of carapace formed by midline slope of vertebral V and midline sulcus of anal scutes (PG), anal notch depth (AN), length of interfemoral sulcus (IL), shortest distance between inguinal scute and pectoral-abdominal sulcus (IE), anterior plastral lobe width (PW), posterior plastral lobe width (XW), taper of anal scutes measured as the angle formed by posterior extension of lines along the lateral edge of the anal scutes (AA), epiplastron thickness at mid-humeral scute (ET), depth of epiplastral lip measured as the distance between the anterior tip of the intergular sulcus and a line formed by resting a straightedge across the dorsal epiplastral lip (EP), cervical scute recession measured from anterior tip of cervical scute to a straight line along the anterior tip of first pair of marginals (NR), ventral extension of posterior carapace measured from posterior tip of interanal sulcus to posterior edge of vertebral V (AV) and to posterior tip of intermarginal XII sulcus (AP), head width at anterior margin of tympanum (HW), length of cusps on upper tomium (LC), greatest width of supratemporal stripe (SS), and width of post-symphyseal (ventral) stripe at level of tympanum (GS).

For multivariate analysis, only turtles with a midline carapace length > 120 mm were included, and males and females were analyzed separately. That reduced the effects of ontogenetic and sexually dimorphic character variation, which may be pronounced in *Pseudemys* (Iverson and Graham 1990). Principal components analysis (PCA-SAS;

Table 1. Qualitative characters used for initial identification of *Pseudemys* species.

P. rubriventris

1. Upper jaw with a prominent notch bordered on each side by tooth-like (tomiodont) cusps (Carr 1952, Crenshaw 1955, Ernst and Barbour 1989).
2. Second pleural scute without C-shaped mark.
3. Plastron red or faded pink with central dark figure extending along seams (Carr 1952, Crenshaw 1955, Ernst and Barbour 1989).
4. Carapace of large individuals with numerous lateral rugosities but flat or concave along the vertebrals (Ernst and Barbour 1989, Weaver and Rose 1967).
5. Dark markings on bridge, including inguinal scute.
6. Posterior (after bridge) inframarginal spots or circles do not overlap intermarginal seams (Ward 1984).
7. Posterior margin of carapace weakly serrated and marginal notches weak.

P. concinna

1. Upper jaw with a very weak notch, not bordered by tooth-like cusps.
2. Second pleural scute with C-shaped mark (Carr 1952, Crenshaw 1955, Ernst and Barbour 1989).
3. Plastron yellow or orange with central dark figure extending along seams.
4. Carapace of large individuals slightly keeled along vertebrals; carapace not finely rugose.
5. Dark markings on bridge, including inguinal scute.
6. Posterior inframarginal circles overlap intermarginal seams.
7. Posterior margin of carapace serrated and marginals prominently notched (Weaver and Rose 1967, Ward 1984).

P. floridana

1. Upper jaw entirely smooth, no notch or cusps.
2. Second pleural scute without C-shaped mark.
3. Plastron pale yellow without any dark markings.
4. Carapace of large individuals rounded or flat (not keeled) along vertebrals.
5. Dark markings usually absent from bridge and inguinal scute (Ward 1984).
6. Markings usually very faint or absent on posterior inframarginals.
7. Posterior margin of carapace weakly serrated and marginal notches weak.

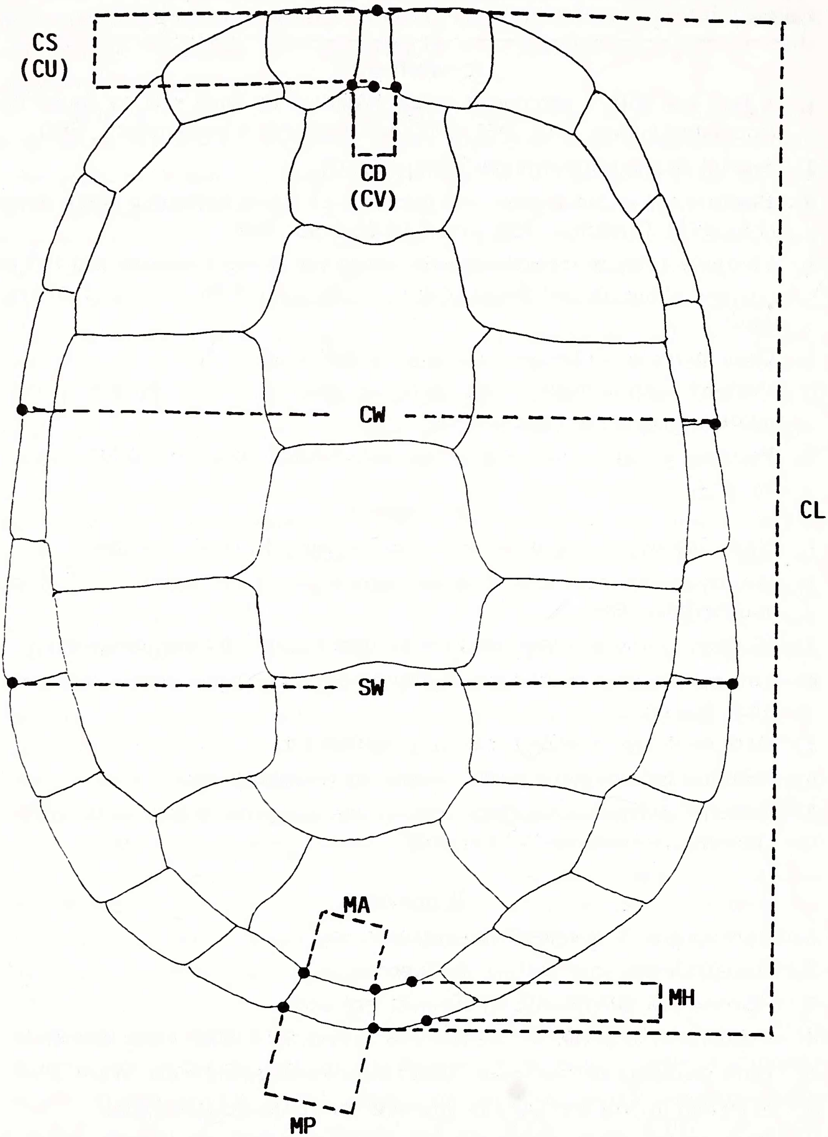

Fig. 2. Illustration of morphometric characters measured on carapace: CS = cervical scute dorsal length, CU = cervical scute ventral length, CD = cervical scute dorsal width, CV = cervical scute ventral width, CW = anterior carapace width, SW = posterior carapace width, CL = carapace length, MA = anterior marginal XII width, MP = posterior marginal XII width, MH = marginal XII length. All measurements are between the appropriate dots.

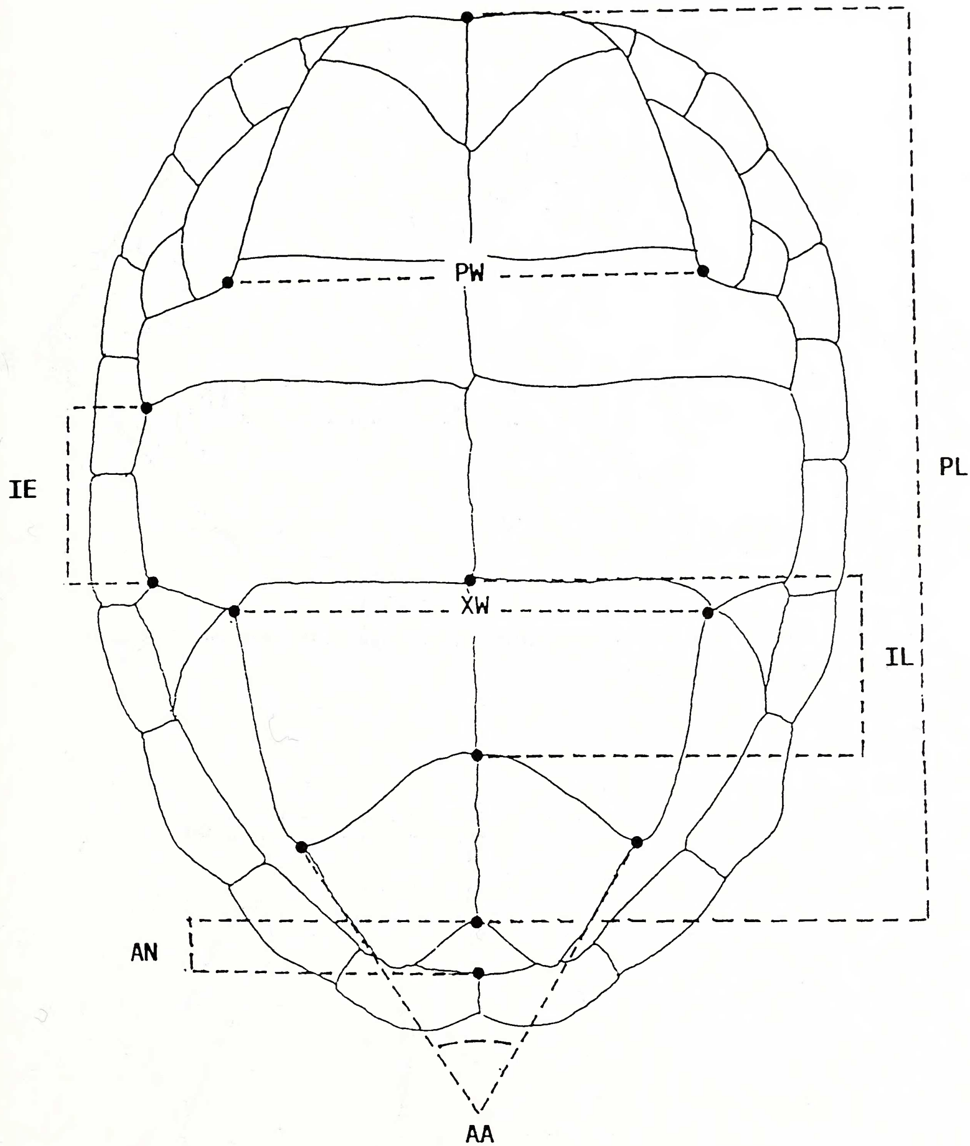

Fig. 3. Illustration of morphometric characters measured on plastron: PW = anterior plastral lobe width, PL = plastron length, XW = posterior plastral lobe width, IE = distance between inguinal scute and pectoral-abdominal sulcus, IL = length of interfermoral sulcus, AN = anal notch depth, AA = lateral angle of anal scutes.

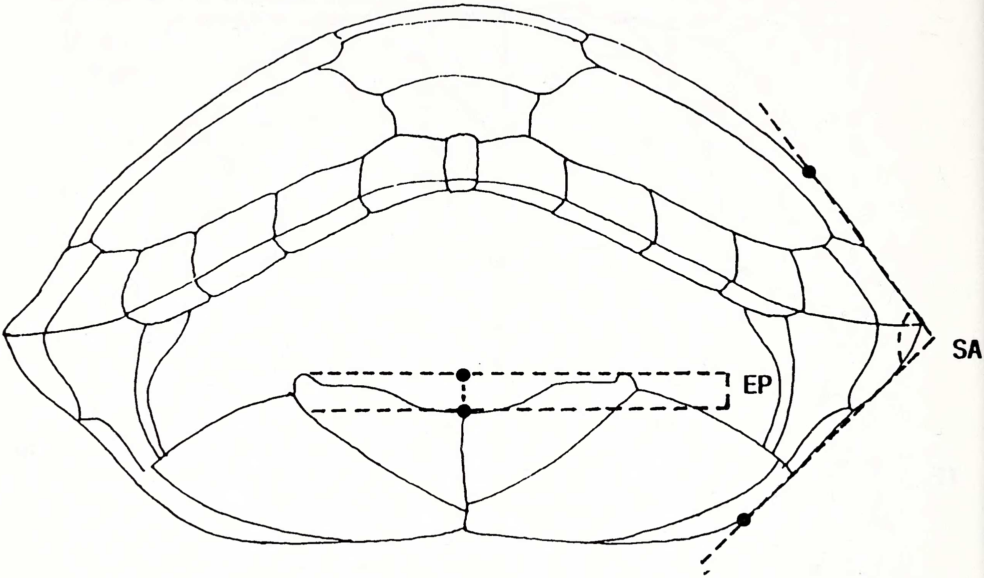

Fig. 4. Anterior view of shell illustrating lateral angle of the carapace (SA) and depth of epiplastral lip (EP).

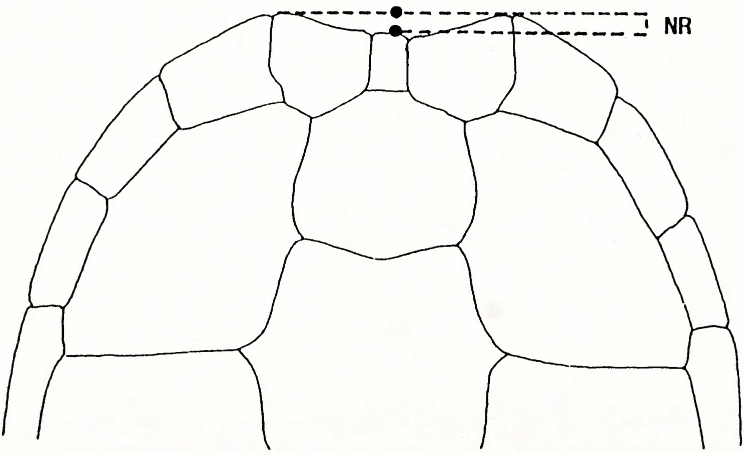

Fig. 5. Dorsal anterior view of the carapace illustrating recession of the cervical scute (NR).

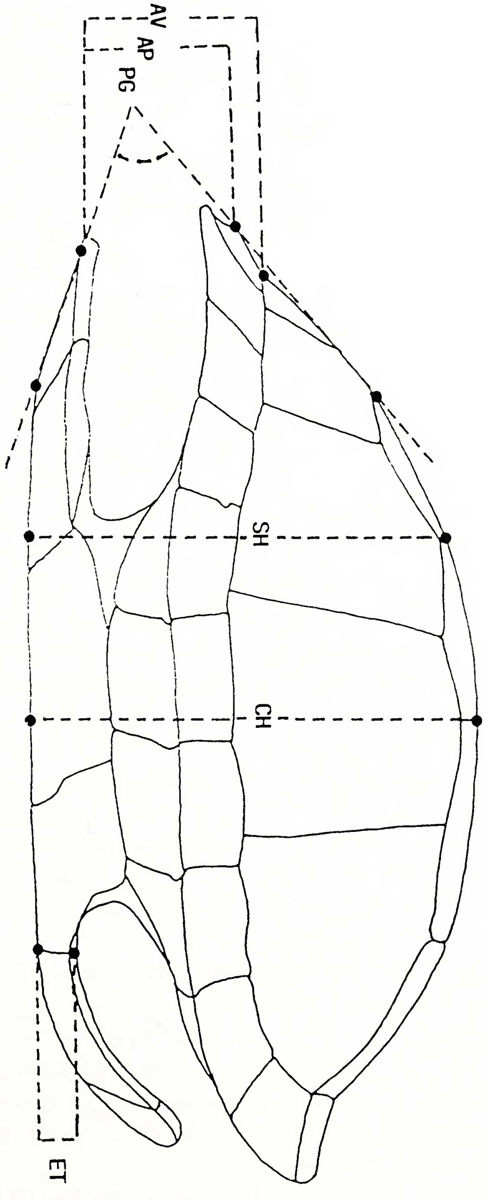

Fig. 6. Lateral view of shell illustrating morphometric characters: CH = anterior shell height, SH = posterior shell height, ET = thickness of epiplastron, AV and AP = ventral extension of posterior carapace, PG = posterior slope (angle) of carapace.

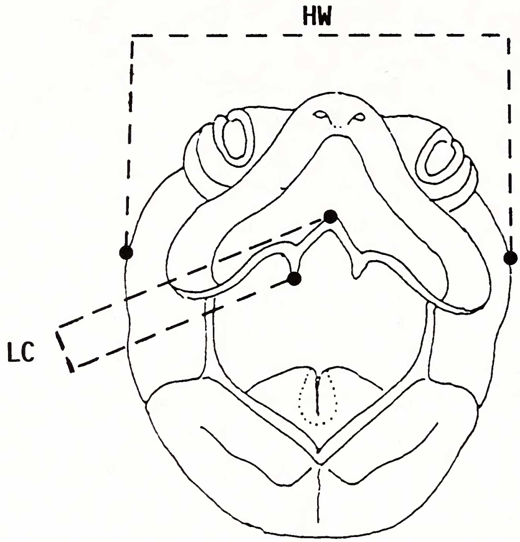

Fig. 7A. Anterior view of the head illustrating length of the tomial cusp (LC) and head width (HW).

Barr et al. 1976) was initially applied, thus avoiding assignment of individuals to groups (species). Morphological similarity or divergence was examined by observing clustering of individuals on bivariate plots of their principal component scores. That provided a test to determine if a priori species identifications based on qualitative characters could be corroborated by mensural characters. It also provided a more objective means to determine morphological overlap between species and possible cases of hybridization or intergradation. If the a priori assignment of a specimen had been noted as questionable (based on qualitative characters) and its PCA plot was clearly outside its species cluster but within the range of another species, it was reidentified. Otherwise, taxonomic reassignment was avoided. Principal components analysis was followed by stepwise discriminant analysis (BMDP7M, Dixon 1977). Discriminant analysis was applied to test for significant morphometric differences between *P. rubriventris*, *P. concinna*, and *P. floridana*. Sexes were again examined separately and the influence of size (age) was reduced by linear regression. Size-adjusted residuals were obtained from the 30 shell and head-stripe measurements by regressing each character on carapace length.

Multivariate analysis of variance (MANOVA-SAS) followed by Fisher's protected least significant difference (*t*-tests) were used to test for utilitarian taxonomic characters that might provide a more objective

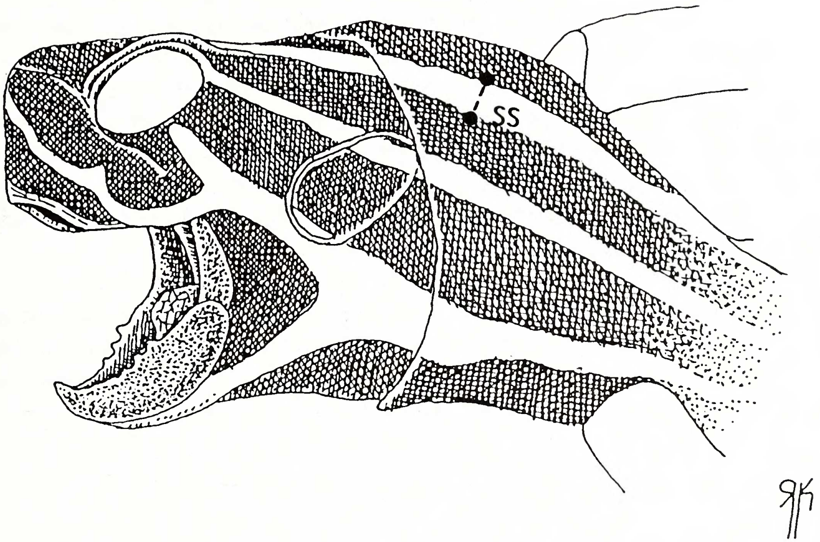

Fig. 7B. Lateral view of the head and neck illustrating maximum width of the supratemporal stripe (SS).

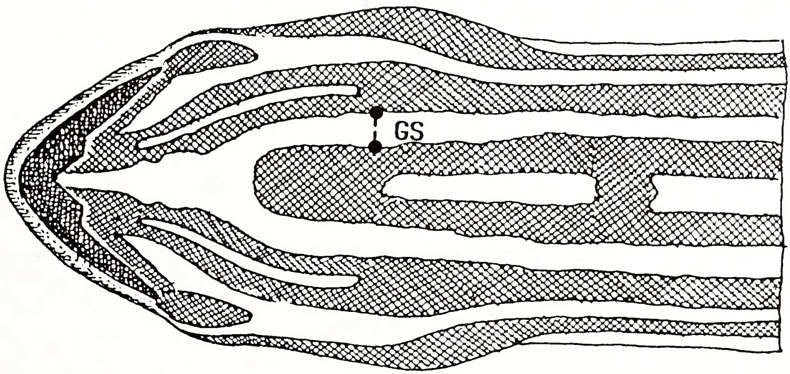

Fig. 7C. Ventral view of the head and neck illustrating width of the post-symphyseal stripe at level of tympanum (GS).

(quantitative) means for identifying species of *Pseudemys*. Thirty character ratios were constructed from 27 of the original 30 characters. These included character ratios that have been reported to be useful in discriminating between *P. concinna*, *P. floridana*, and *P. rubriventris*. Sexes were again treated separately. Although several of these ratios are somewhat redundant and therefore strongly correlated, each was examined to allow direct comparisons with previously reported values (e.g. Ward 1984). Despite the theoretical problems with using ratios in statistical analyses, their effectiveness in taxonomic studies of turtles has been clearly demonstrated (Iverson and Graham 1990).

We also examined large series of hatchling and juvenile *P. rubriventris*, *P. floridana*, and *P. concinna*. Young individuals were very difficult to identify. Characters that we found to be diagnostic in adults of these species were either impossible to resolve in young turtles or extremely variable, even within a single brood of hatchlings.

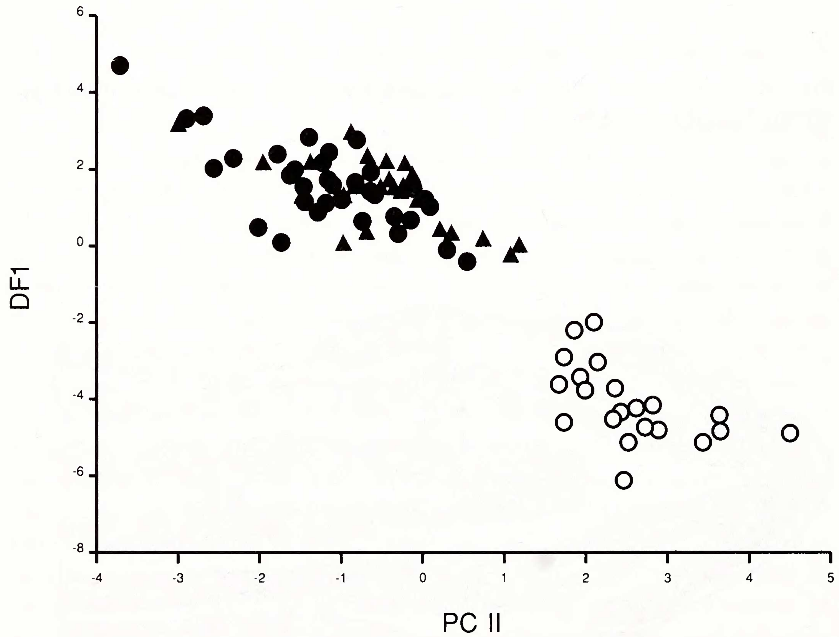

Fig. 8. Plot of individual adult male *Pseudemys* based on principal components analysis (PC II) and discriminant function analysis (DF 1) of morphometric characters (see text). Open circles represent *P. rubriventris*, closed circles represent *P. concinna*, and triangles represent *P. floridana*.

STATISTICAL RESULTS

The first factor (PC I) extracted by principal components analysis was size-related, as expected (Wiley 1981). It accounted for more than 50% of the total variance in male and female turtles and all loading coefficients (eigenvectors) were high and positive (except angle of anal scute, AA). PC II accounted for 24 and 26% of the remaining variance, respectively, by sex. Among the 30 components extracted, only PC II showed evidence of clustering by species. When individuals were plotted according to their PC II scores (Fig. 8 and 9), *P. rubriventris* showed distinct separation from *P. concinna* and *P. floridana*, which clustered together and did not appear morphologically distinct. The most influential mensural characters loaded on PC II are identified in Table 2. Two male specimens (NCSM 11365 and 13812) from extreme northeastern North Carolina (Gates Co.) had been tentatively identified as *P. rubriventris*. Because these two individuals plotted well outside the

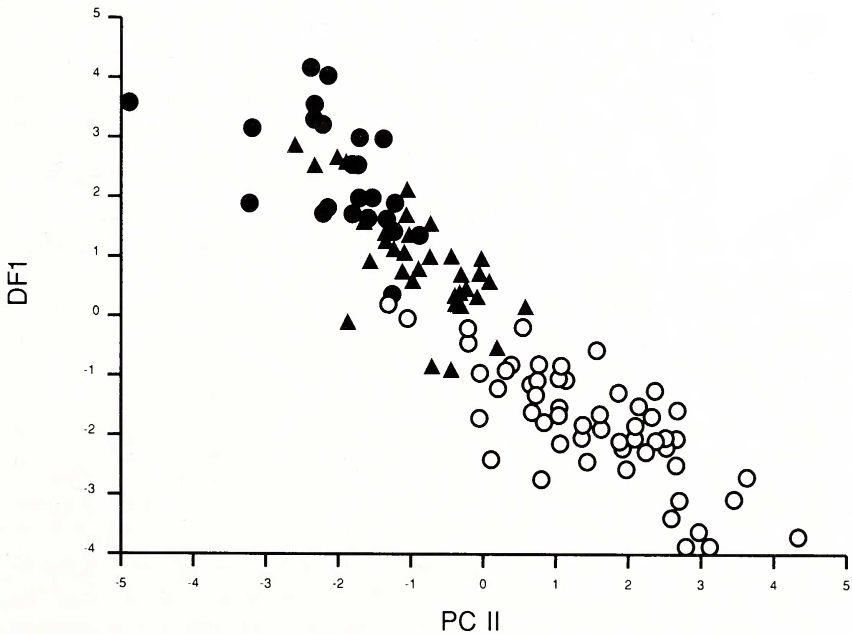

Fig. 9. Plot of individual adult female *Pseudemys* based on principal components analysis (PC II) and discriminant function analysis (DF 1) of morphometric characters. Open circles represent *P. rubriventris*, closed circles represent *P. concinna*, and triangles represent *P. floridana*.

range of *P. rubriventris* on PC II and within the range of *P. floridana*, they were reidentified as *P. floridana*. Another male specimen (NCSM 28704) from the same general area (Beaufort Co., N.C.) had been tentatively identified as *P. floridana*, but because it plotted within the range of *P. rubriventris* on PC II, it was reassigned to the latter species for further analysis.

Discriminant analysis of male and female *Pseudemys* also revealed marked separation between *P. rubriventris* and the other two congeners (Fig. 8 and 9). Eighty-eight percent (females) and ninety-four percent (males) of the variance was explained by the first discriminant function (DF 1). Coefficients for the most influential characters are listed in Table 2. Although differences ($P<0.05$) were found between all three species, significance values were much larger comparing *P. rubriventris* with *P. concinna* and *P. floridana* (F = 18-42) than comparing *P. concinna* with *P. floridana* (F = 3.0 and 6.9). For males, 100% of the *P. rubriventris* were classified (by group discriminant function) correctly, whereas there was a 17-18% classification error between *P. concinna* and *P. floridana*. For females, 87% of the *P. rubriventris*, 78% of the *P. concinna*, and 80% of the *P. floridana* were correctly grouped.

Table 2. Coefficients and factor loadings for the most influential morphometric characters of discriminant analysis (DF 1) and principal components analysis (PC II).

	DF 1		PC II	
	MALE	FEMALE	MALE	FEMALE
Plastron length (PL)	0.33			
Cervical scute dorsal length (CS)			0.17	0.17
Cervical scute ventral length (CU)		-0.40	0.26	0.30
Marginal scute XII length (MH)	0.41	0.42		
Lateral angle of carapace (SA)	-0.29		0.24	0.25
Anal notch depth (AN)			-0.15	-0.20
Taper (angle) of anal scutes (AA)	-0.42		0.44	0.33
Ventral posterior extension of carapace (AP)		0.57	-0.18	-0.15
Length of tomial cusps (LC)	0.91	-0.45	0.42	0.45
Supratemporal stripe width (SS)		0.54	-0.43	-0.41
Post-symphyseal stripe width (GS)			-0.31	-0.41

Multivariate analysis of variance (Wilks' criterion) for 30 character ratios and 3 unadjusted characters indicated significant differences ($P<0.01$) between species. Differences ($P<0.01$) were found in 15 characters for males and 15 characters for females. Fisher's test indicated that most of these characters separate *P. rubriventris* from *P. concinna* and *P. floridana* (Table 3). The only characters that separate *P. concinna* and *P. floridana* are based on head and neck markings and shell height ($P<0.05$). The following characters and character ratios showed no significant difference ($P>0.05$) between species: PG, CW/CL, CD/CL, CD/CW, CD/SW, CV/CD, MA/MD, MP/MH, MH/MA, IL/PL, IE/CL, PX/XW, XW/PL, ET/PL, EP/PL, NR/CL.

CHARACTER ANALYSIS

Morphometric analysis of *P. rubriventris*, *P. concinna*, and *P. floridana* revealed several measurements that distinguish those species in northern and middle Atlantic slope drainages. In all *Pseudemys*, females have considerably deeper shells than males. However, interspecific comparisons of the same sex indicated a deep shell (SH and CH) in *P. rubriventris*, an intermediate depth in *P. floridana*, and a shallow shell in *P. concinna* (Table 3). These results are similar to differences in shell height reported by Seidel (1981), Ward (1984), and Weaver and Rose (1967). Head-striping patterns also distinguish these three forms. The broadest gular (post-symphyseal) stripes (GS) and supratemporal stripes (SS) are seen in *P. concinna*, moderate stripes are found in *P. floridana*, and the narrowest stripes occur in *P. rubriventris* (Table 3, Fig. 10). Several additional mensural characters distinguish *P. rubriventris* from *P. concinna* and *P. floridana*, but do not separate those two from each other. Compared with *P. concinna* and *P. floridana*, *P. rubriventris* has a longer cervical scute (CU, CS), shallower anal notch (AN), broader anal scute angle (AA), wider lateral angle (slope) of carapace (SA), greater ventral extension of the posterior carapace (AV, AP), greater head width (HW), and longer tomial cusps (LC) (Fig. 11 and 12). A long cervical scute and prominent tomial cusps have frequently been cited as diagnostic characteristics of the redbelly turtles, *P. rubriventris*, *P. nelsoni*, and *P. alabamensis* (Carr 1952, Weaver and Rose 1967, Ward 1984). Weaver and Rose (1967) noted ventral projection of the carapace (pygal bone) in *P. rubriventris* but not in *P. concinna* and *P. floridana*, and Ward (1984) reported a deeper anal notch in *P. concinna* and *P. floridana* compared with redbelly turtles. Angle of the anal scute (xiphiplastron) is a characteristic that shows pronounced sexual dimorphism (Fig. 12).

Ward (1984) described the following scute and shell characters that reportedly distinguish *P. floridana* from *P. concinna*: wider cervical

Table 3. Morphometric characters useful in distinguishing species of *Pseudemys* in Atlantic Coast drainages.[a]

Species	*P. rubriventris*		*P. concinna*		*P. floridana*	
Sex	M	F	M	F	M	F
N	21	55	34	23	24	35
PL/CL (X100)	90.2±3.5(86-101)	93.0±2.3(88-100)	88.4±2.5(83-94)	91.4±1.8(88-95)	87.3±1.8(83-91)	91.2±2.0(86-96)
CH/CW (X100)	51.6±4.0(45-61)		47.4±5.0(33-56)*		50.1±2.8(46-59)*	
CH/SW (X100)	49.3±3.7(45-58)	54.2±4.3(46-66)	44.6±4.6(31-53)*	50.7±4.4(38-58)	47.2±2.6(43-54)*	
CH/CL (X100)	35.9±2.7(31-44)		33.5±2.5(29-38)*		35.4±1.6(33-38)*	
SH/CL (X100)	33.4±2.2(30-39)	36.6±2.1(32-42)	31.3±2.3(27-35)*	35.8±2.5(30-39)*	32.6±1.4(30-35)*	36.7±2.4(32-42)*
SW/CL (X100)		72.3±4.3(65-82)		74.6±2.8(70-82)		74.9±2.7(70-80)
CU/CS (X100)	55.7±9.4(39-74)	54.2±9.0(39-78)	40.2±13.3(19-101)	42.3±8.3(31-66)	45.0±8.7(31-63)	46.3±9.1(29-74)
CS/CL (X100)	8.5±0.7(7-11)	8.3±0.8(6-10)	7.4±0.9(5-9)	7.3±0.8(6-9)	7.6±0.9(5-10)	7.6±0.7(5-10)
AV/AP (X100)	109.9±9.2(98-136)	116.8±10.4(96-139)	98.8±7.3(88-112)	102±7.4(87-117)	99.8±4.9(94-113)	106.4±9.4(95-141)
AP/CL (X100)	13.6±2.5(10-23)	12.2±1.7(9-16)	14.9±1.5(12-20)	13.7±1.6(10-17)	14.9±0.9(13-17)	13.3±1.6(10-17)
AN/PL (X100)	3.3±0.7(2-6)	3.2±1.0(1-5)	3.9±1.0(2-7)	4.2±1.8(2-12)	4.2±0.8(3-6)	3.8±0.9(2-6)
AA	6.8±8.3(45-80)	71.5±10.5(50-99)	49.1±9.4(30-72)	61.2±6.3(52-75)	49.5±10.1(30-65)	63.5±9.0(45-80)
SA	105.7±13.5(65-121)	113.4±11.5(82-139)	88.5±11.8(57-110)	101.2±11.7(70-120)	91.1±9.3(72-105)	106.9±9.9(80-124)
HW/CL (X100)	13.7±1.2(12-18)	13.7±1.0(12-16)	12.5±1.1(11-17)	12.6±0.8(11-15)	12.8±0.7(12-14)	12.9±0.8(11-15)
LC/HW (X100)	4.2±1.3(0-6)	3.7±1.6(0-8)	0.2±0.9(0-4)	0.2±0.9(0-4)	0.2±0.8(0-3)	0.4±1.0(0-5)
SS/HW (X100)	7.5±1.9(5-12)	6.4±2.3(3-15)	14.9±3.1(8-23)*	13.6±3.2(8-19)*	12.4±3.2(8-19)*	9.8±3.0(4-19)*
GS/HW (X100)	7.1±1.6(4-11)	5.8±1.8(2-13)	10.8±2.0(6-16)*	10.3±1.8(7-15)*	9.1±2.8(5-14)*	8.8±2.2(4-13)*

[a]Mean is followed by ± one standard deviation, and range is in parentheses. Symbols for characters and ratios are defined in text. Comparing ratio means (within sex) of *P. rubriventris* with the other two species, significant differences ($P<0.05$) were found for all characters except shell height (CH and SH) in *P. floridana*. An asterisk (*) indicates that means are significantly different between *P. concinna* and *P. floridana*.

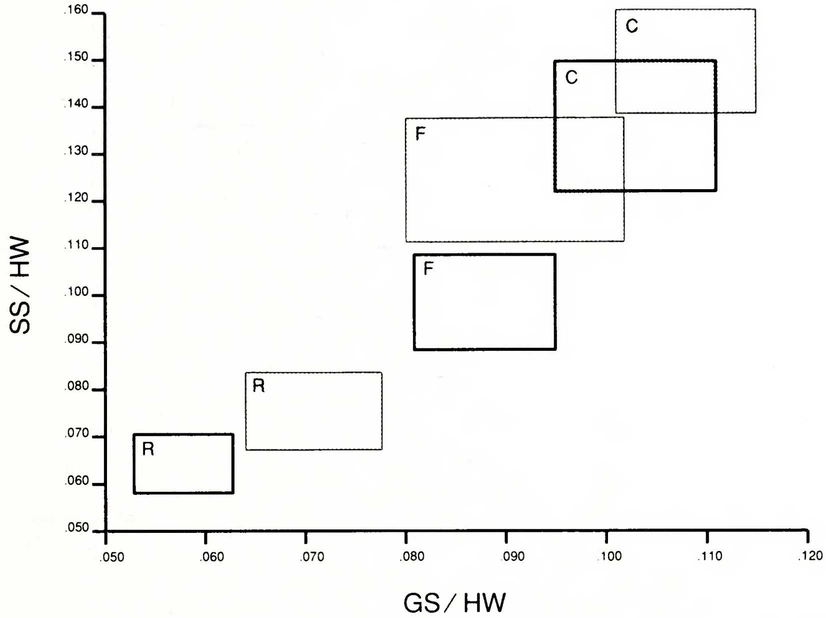

Fig. 10. Graph of post-symphyseal stripe width/head width (GS/HW) versus supratemporal stripe width/head width (SS/HW). Open rectangles (females) and shaded rectangles (males) are formed by lines two standard errors above and two standard errors below means. C = *P. concinna*, F = *P. floridana*, R = *P. rubriventris*.

scute (CD/CL, CD/CW, CD/SW), longer cervical scute underlap-ventral length (CU/CS), greater anterior extension of cervical scute (NR/CL), deeper curve of epiplastron (EP/PS), greater ratio of anterior/posterior width of marginal XII (MA/MP), broader angle of anal scutes (AA), and greater ratio of anterior/posterior plastral lobe width (PW/XW). In our sample that compares *P. concinna concinna* with *P. floridana floridana*, we found no differences in these characters and thus conclude that they have no taxonomic value in separating species in the central Atlantic drainages. Unfortunately, Ward (1984) did not provide a list of the specimens he examined. Most of Ward's characters do appear to separate the Florida subspecies, *P. floridana peninsularis*, from *P. concinna* (personal observation). Therefore, we assume that Ward's interspecific comparisons of *P. floridana* were based primarily or exclusively on character analysis of *P. f. peninsularis*.

Many of the qualitative characters that have been used to define species of *Pseudemys* show considerable intraspecific variation in Atlantic slope populations. Among 15 characters recorded, only five were found to have taxonomic value. Of the *P. concinna* examined, 63% showed

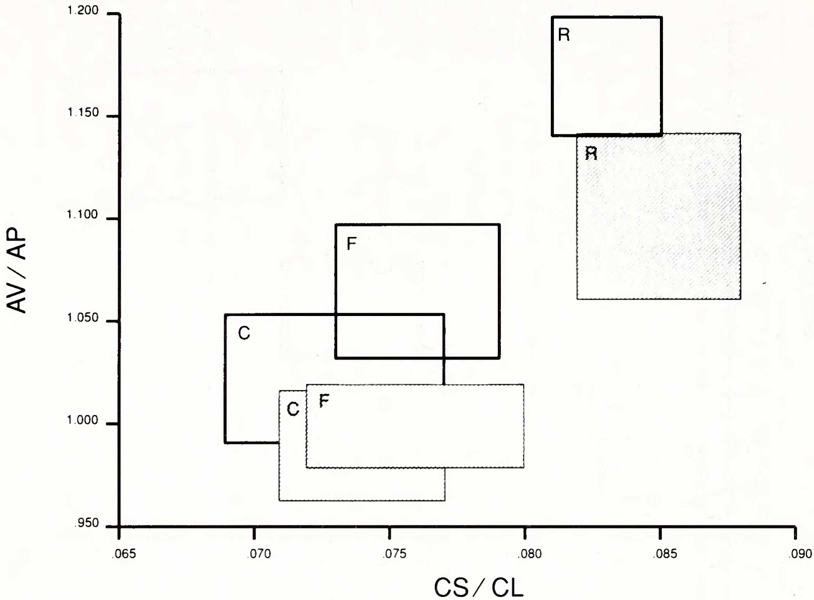

Fig. 11. Graph of cervical scute length/carapace length (CS/CL) versus ventral extension of posterior carapace (AV/AP). Symbols are defined in Fig. 10.

evidence of a C-shaped mark on the second pleural scute, whereas only 6% of the *P. floridana* and 4% of the *P. rubriventris* had this marking. As reported in earlier literature, the lateral yellow lines on the pleural scutes of *P. floridana* (Fig. 14) form irregular bands or bars, whereas these markings are more circular, forming ocelli, in *P. concinna* (Fig. 13). A dark figure on the plastron was detected in 61% of the *P. rubriventris* and 35% of the *P. concinna* (Fig. 15), whereas 96% of the *P. floridana* showed no evidence of plastral markings (Fig. 16). The submarginal circles anterior to the bridge were solid (spots) in 42% of the *P. rubriventris*, 28% of the *P. floridana*, and 6% of the *P. concinna*. Ward (1984) reported that the anterior submarginal spots are solid blotches in *P. floridana*, whereas in our sample, 72% of the *P. floridana* had open circles. The apex of the lower jaw (viewed ventrally) was rounded, not angled, in 51% of the *P. rubriventris*, 2% of the *P. floridana*, and in none of the *P. concinna*. There were more than 11 prominent head stripes (at level of the posterior margin of the tympanum) in 94% of the *P. concinna*, 10% of the *P. rubriventris*, and 6% of the *P. floridana* examined.

As in the mensural characters, several of the qualitative characters that reportedly distinguish these species do not effectively separate them in the central Atlantic coast drainages. Ward (1984) stated in his

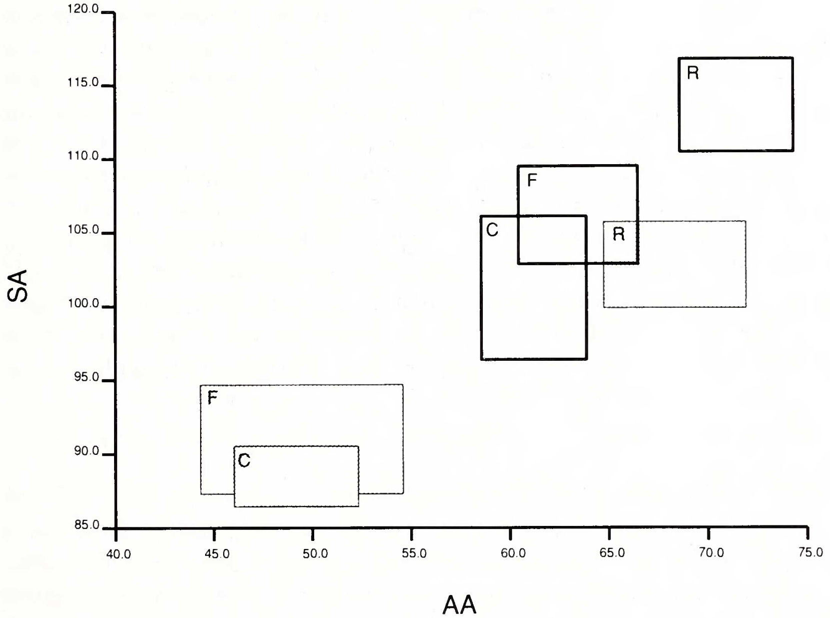

Fig. 12. Graph of lateral angle of carapace (SA) versus angle of anal scutes (AA). Symbols are defined in Fig. 10.

definition of the subgenus *Ptychemys* that redbelly turtles (including *P. rubriventris*) have posterior marginals without a notch. Of the *P. rubriventris* we examined, 62% had posterior marginals that were serrated (offset at seam) and clearly notched. Ward (1984) and Weaver and Rose (1967) reported that the redbelly turtles (in contrast to *P. concinna* and *P. floridana*) have a strongly rugose carapace (Fig. 17), occasionally even as juveniles. In our sample, we found pronounced carapacial rugosity in 22% of the *P. concinna*, 45% of the *P. floridana*, and 49% of the *P. rubriventris*. These rugosities were observed exclusively in large (old) adults. Ward (1984) reported that the inguinal scute of *P. floridana* (in contrast to *P. rubriventris* and *P. concinna*) lacks any black markings. We found that 74% of the *P. floridana* in our sample had black markings on the inguinal scute. However, these markings are usually absent in *P. f. peninsularis* (personal observation). Ward also reported that inframarginal spots posterior to the bridge are mostly confined anterior to the seam in *P. floridana*. In 40% of the *P. floridana* we examined, these inframarginal spots broadly overlap the seams.

In old male *Pseudemys* from the Atlantic drainage areas, melanism was detected in 2% of the *P. floridana*, 6% of the *P. concinna*, and 29% of the *P. rubriventris*. Melanism in *P. rubriventris* was not only more frequent, but also more complete compared with the other two species.

The pattern of male melanism observed in all species was a loss of yellow lines on the soft parts and carapace and development of a reticulated (worm-like) pattern of dark speckled markings on the head, carapace, and plastron (Fig. 18). This pattern is quite different from the melanism that develops in populations of *Trachemys scripta* (Lovich et al. 1990), but similar to that of the Cuban slider, *Trachemys decussata decussata* (Seidel 1988). A different form of melanism is found in adult female and young male *P. rubriventris* in northern portions of their range (Pennsylvania and New Jersey). In those areas, the soft parts and carapace become nearly solid black, but the plastron remains bright coral or red. It is interesting that darkening to this extent and loss of yellow lines apparently do not occur in the southern populations in Virginia and North Carolina.

DISCUSSION

Morphological divergence between *P. concinna* and *P. floridana* is much less than their collective divergence from *P. rubriventris*. Neither principal components analysis nor discriminant analysis clearly separated the two former taxa from each other (Fig. 8 and 9). Male specimens of *P. rubriventris* showed no overlap with *P. concinna* and *P. floridana*, but some overlap was observed for females. Six female *P. rubriventris* (NCSM 20166, 28753, 28897, 29278; AMNH 90644; USNM Field Series 159366) and two female *P. floridana* (NCSM 14783; CM Field Series 24447) plotted intermediately between species clusters (Fig. 9). Specific identification of all these individuals was originally noted as questionable, and all were collected from the relatively small area of southeastern Virginia and northeastern North Carolina where the ranges of these species overlap. There is little doubt that *P. rubriventris* in the southern portion of its range is somewhat morphologically convergent with *P. floridana*. One possible explanation for this is that reproductive isolation is not complete and a limited amount of gene flow occurs between these species. That would support Crenshaw's (1965) proposal of hybridization in the region. Another explanation is that selection pressures are similar in this area of sympatry, resulting in homoplastic (convergent) character states (as suggested for other geographic regions by Carr 1952 and Ward 1984).

Two of the morphologically intermediate specimens from northeastern North Carolina (NCSM 29278 from Dare Co. and 14783 from Gates Co.) strongly suggest hybridization of *P. rubriventris* with other *Pseudemys*. Skulls were prepared from these two turtles to examine osteological characters that have been used to distinguish *P. rubriventris* from *P. concinna* and *P. floridana* (McDowell 1964, Ward 1984). One specimen (NCSM 29278) is an adult female (315 mm carapace length) with a "C" on the second pleural scute and broad gular and supratemporal head stripes (13 and 15% of head width) similar to *P. concinna* or *P. floridana*. However, it has a relatively long cervical scute (8% of carapace length), well-defined premaxillary notch, and broad xiphiplastron angle (75°) as in *P. rubriventris*. The skull of that turtle is also clearly intermediate. The vomer marginally contributes to the triturating (alveolar) surface, and the lateral edge of the dentary is weakly serrated. Alveolar width on the dentary surface is 15% of the condylobasal length, and maxillary alveolar width is 21%. In eight *P. rubriventris* skulls that we examined, the dentary width ranged from 17 to 21%, and the maxillary width ranged from 20 to 25%. In 11 *P. concinna* and *P. floridana* examined, the dentary width ranged from 13 to 16%, and the maxillary ranged from 16 to 20%. The other intermediate specimen (NCSM 14783) is an adult female (254 mm carapace length) without a "C" mark on the second pleural scute and with fairly narrow gular and supratemporal stripes (7-8% of head width) as in *P. rubriventris*. However, similar to *P. concinna* and *P. floridana*, the cervical scute is less than 8% of the carapace length, the lateral angle of the carapace is 95°, and the xiphiplastron angle is 55°. The skull of NCSM 14783 is also somewhat intermediate. Although the vomer does not project to the alveolar surface, the lateral edge of the dentary is weakly serrated. Alveolar width on the dentary surface is 17% of the condylobasal length, and the maxillary width is 20%. Both NCSM 29278 and 14783 are thus morphological intermediates (presumed hybrids). The former more closely resembles *P. rubriventris*, whereas the latter is more similar to *P. floridana*.

Ward (1984) indicated that markings and coloration are too variable to be reliable for diagnosing cooter species. If, as Ward suggests, only osteological characters reliably separate *P. concinna* from *P. floridana*, those species should be considered cryptic (sibling) based on their external morphology. That would also imply that there are two clearly recognizable osteomorphs, with little intergradation or polymorphism. Because large series of skeletal material taken throughout the range of *Pseudemys* have not been examined, there is no basis for that conclusion. Hedges (1990) appropriately stated that "speciation is a dynamic process and we should expect borderline cases." Results from the present study suggest that the relationship between *P. concinna* and *P. floridana* in the Atlantic drainages of North Carolina is more characteristic of subspecies than species. Nearly all of the typical examples of *P. concinna* occur in the piedmont, whereas individuals easily identified as *P. floridana* are in the coastal plain (Fig. 1). That is similar to Carr's (1952) observations that led him to consider the two forms subspecies of *P.*

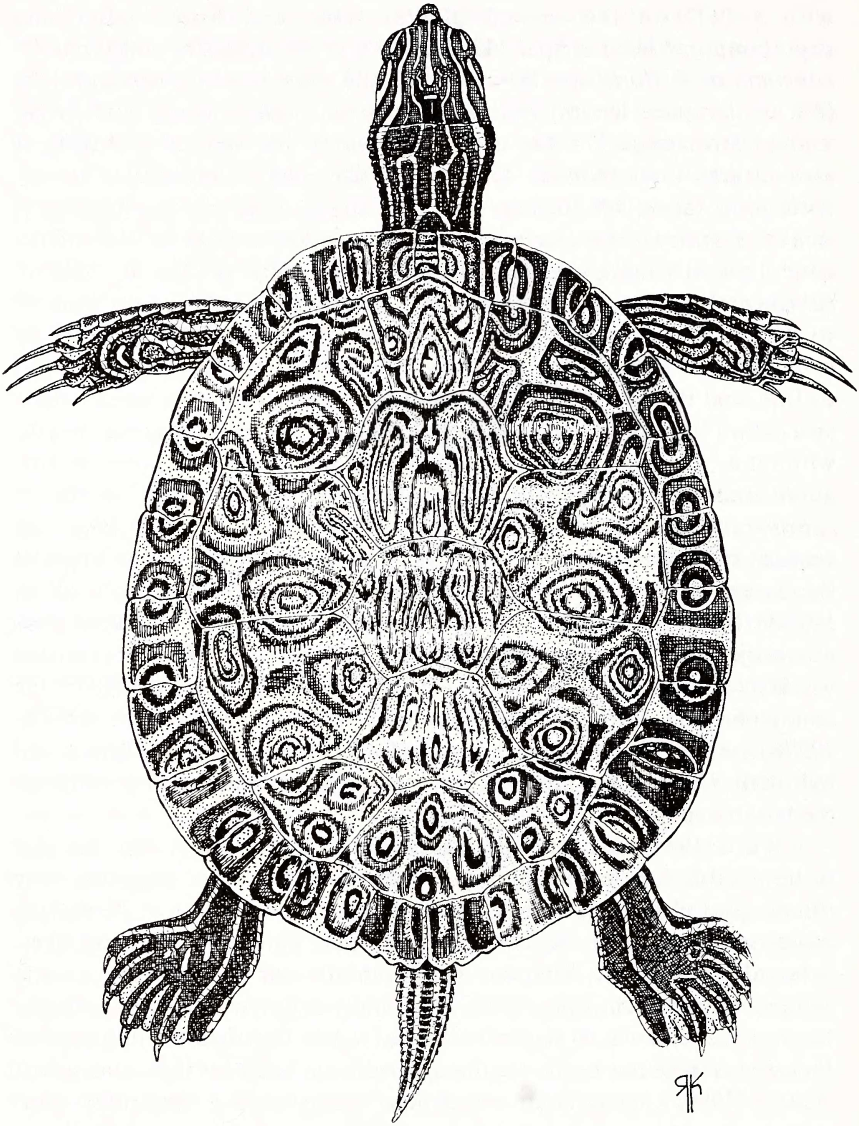

Fig. 13. Dorsal view of a young male *P. concinna* from Guilford Co., N.C. (NCSM 30278).

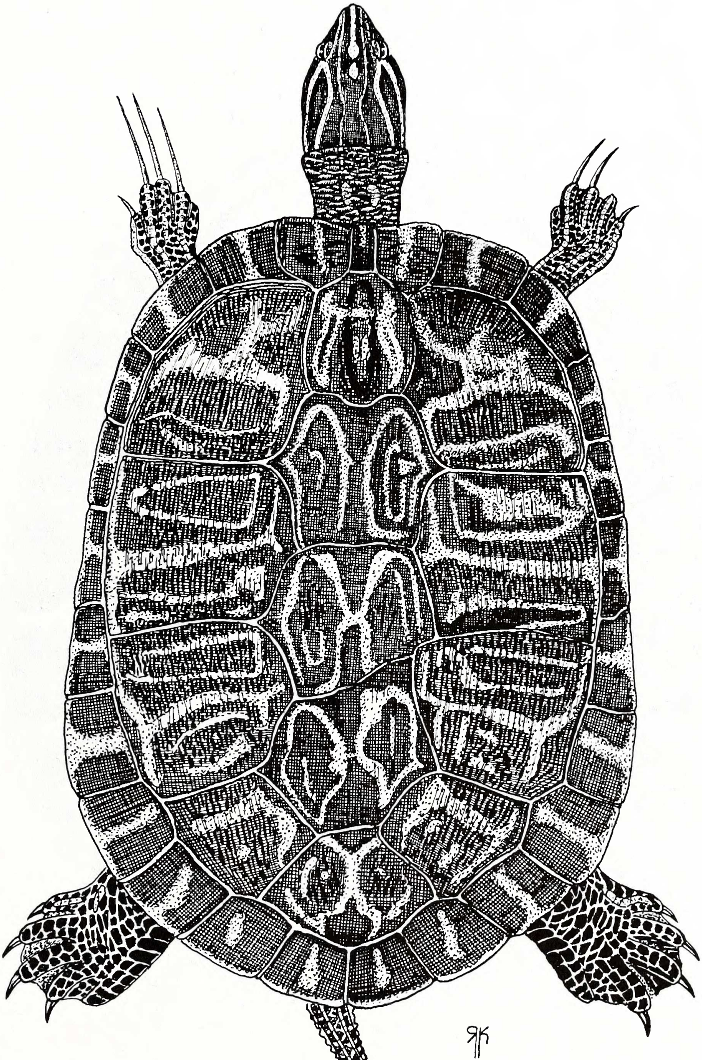

Fig. 14. Dorsal view of an adult male *P. floridana* from Pender Co., N.C. (NCSM 30475).

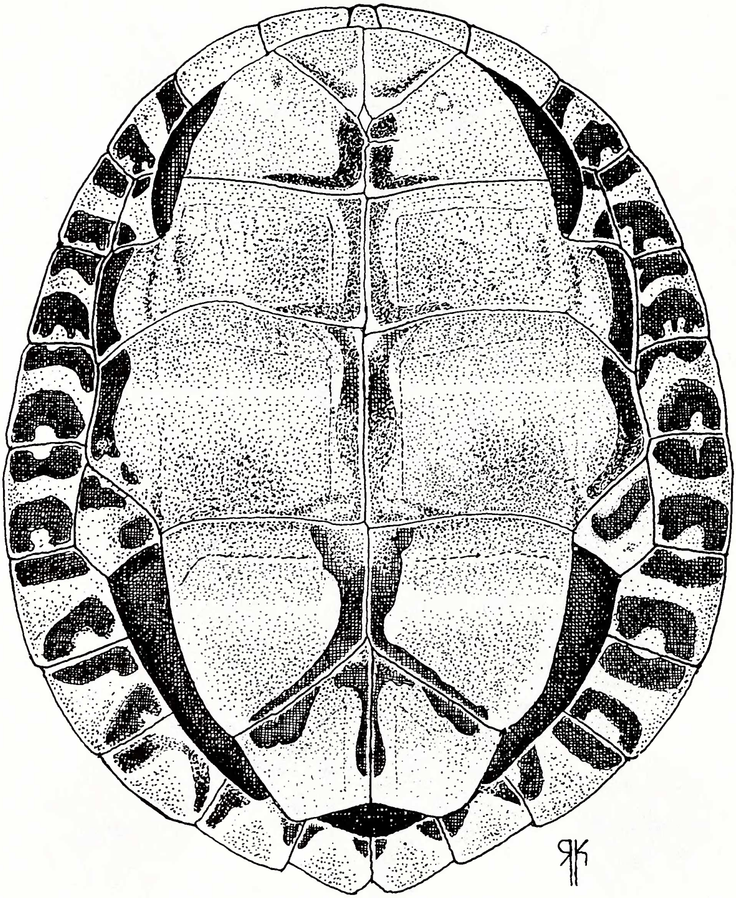

Fig. 15. Plastral view of a young male *P. concinna* from Guilford Co., N.C. (NCSM 30278).

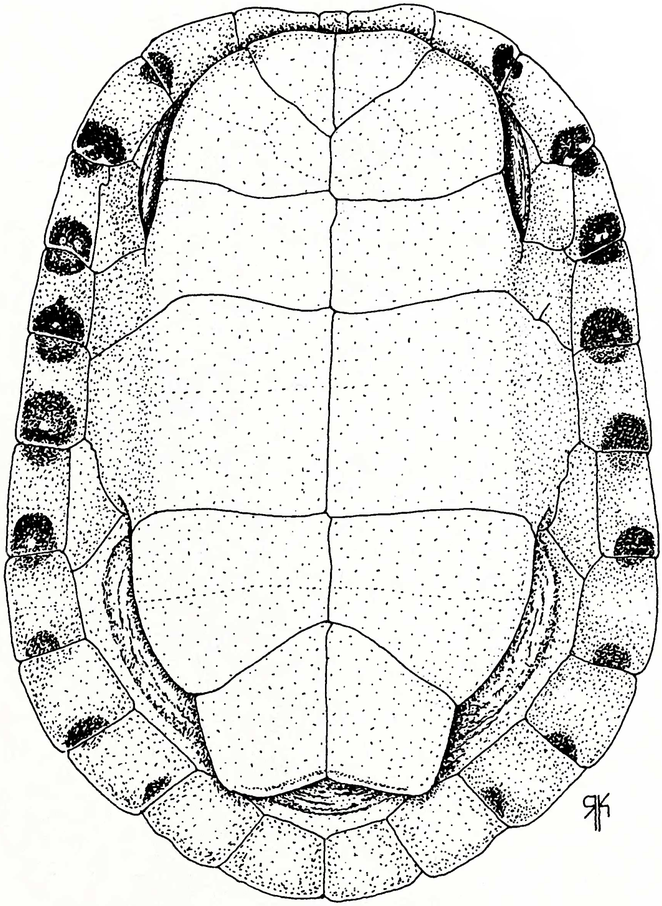

Fig. 16. Plastral view of an adult male *P. floridana* from Pender Co., N.C. (NCSM 30475).

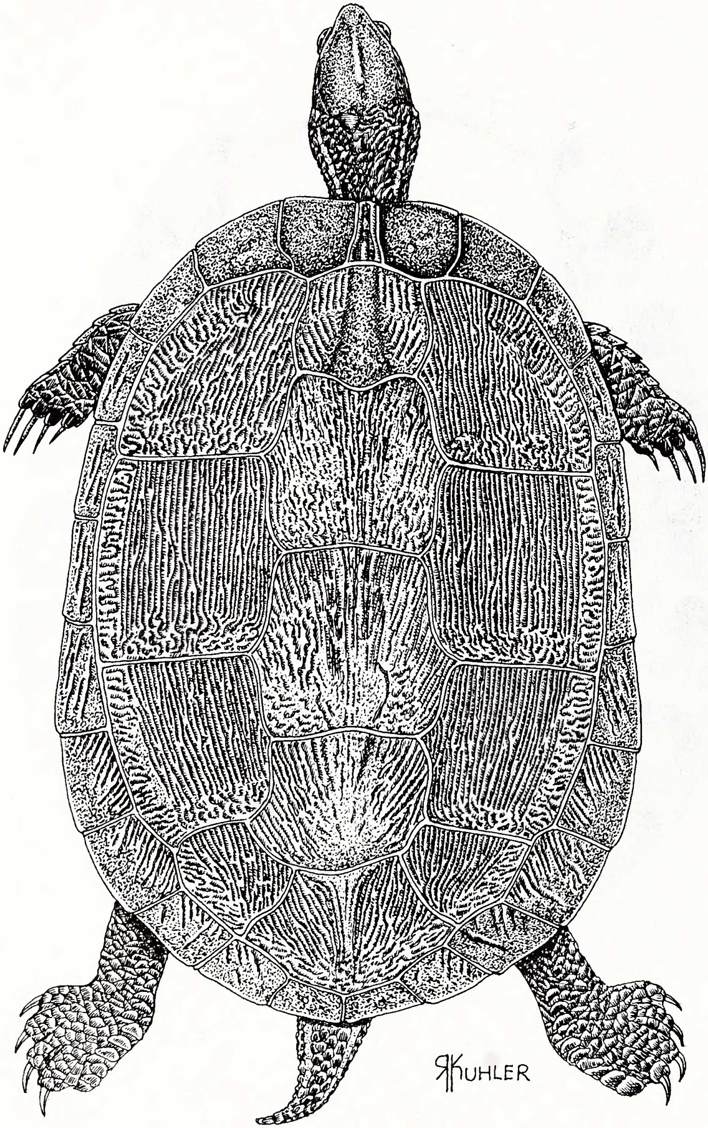

Fig. 17. Dorsal view of an adult melanistic male *P. rubriventris* from Dare Co., N.C. (NCSM 22818).

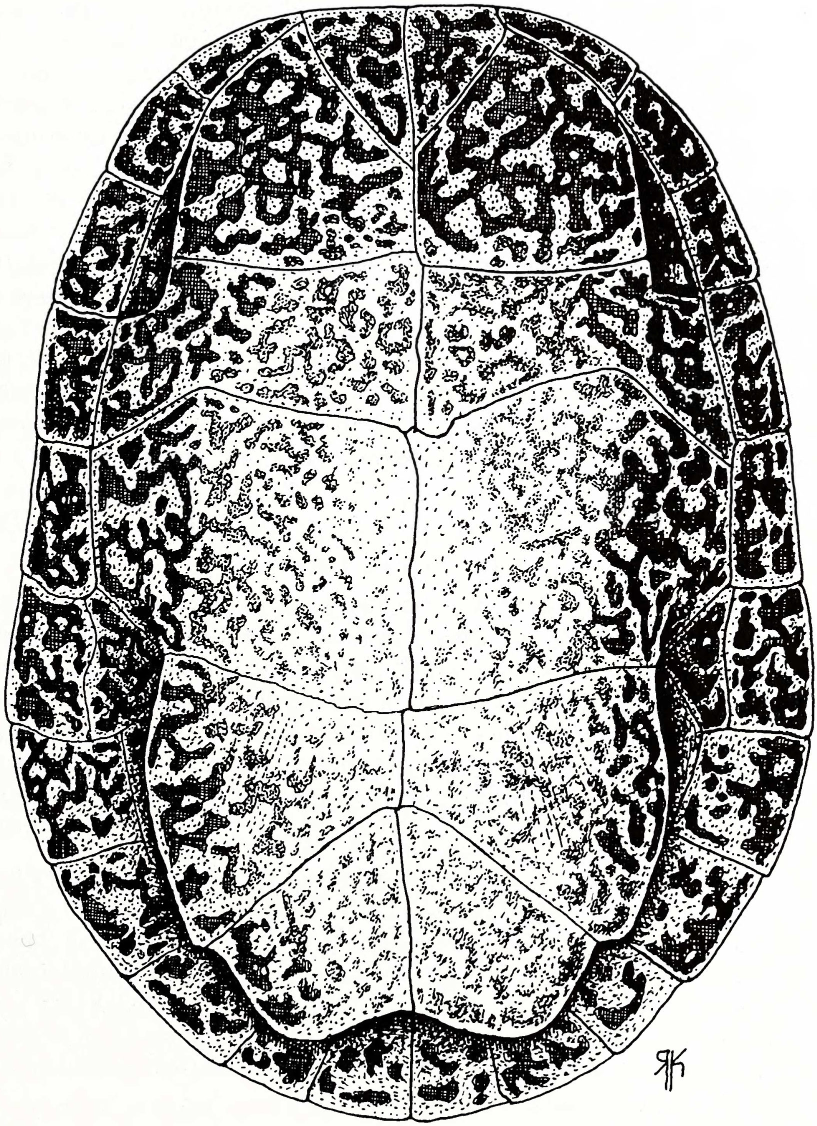

Fig. 18. Plastral view of an adult melanistic male *P. rubriventris* from Dare Co., N.C. (NCSM 22818).

floridana. Many of the specimens in the area of the Fall Line appear to be intermediate between *P. concinna* and *P. floridana*, forming an apparent zone of intergradation. In a few instances typical *P. floridana* and *P. concinna* appear to be in geographic proximity, but they are rarely, if ever, observed in microsympatry. *Pseudemys concinna* is found in rivers or impoundments, and *P. floridana* frequents more lentic habitats, which include backwaters of coastal-plain rivers. Typical examples of these turtles may be distinguished readily by their markings, but there is no consistent external difference in cranial or shell morphology, except perhaps shell depth. Furthermore, some of the diagnostic characters that separate these species elsewhere in their ranges apparently have little diagnostic value for *P. concinna* and *P. floridana* on the Atlantic slope. In spite of these observations, we feel it is premature to propose a conspecific relationship for the two taxa. The senior author (MES) is currently examining morphological variation in *P. floridana* and *P. concinna* throughout their entire ranges. Results from that analysis, particularly an evaluation of *P. f. peninsularis*, should provide critical data for taxonomic decisions.

KEY TO ADULT *PSEUDEMYS* IN ATLANTIC COAST DRAINAGES

1. Upper jaw with prominent notch bordered on each side by tooth-like cusps (length of cusp 3-7% of head width). Gular and supratemporal stripes narrow, 5-8% of head width. Cervical scute long, 8-9% of carapace length. Lateral angle (slope) of carapace steep, 110-117° in females and 100-106° in males. Angle formed by lateral edges of xiphiplastron (anal scutes) broad, 68-75° in females and 64-72° in males. Plastral ground color in living specimens pink or coral. .... *P. rubriventris*

   Upper jaw with only a very shallow notch or notch entirely absent. Cusps either absent or very small (length less than 3% of head width). Gular and supratemporal stripes broad, 8-12% of head width. Cervical scute short, 7-8% of carapace length. Lateral angle (slope) of carapace moderate, 97-109° in females and 87-95° in males. Angle formed by lateral edges of xiphiplastron (anal scutes) sharp, 58-67° in females and 44-55° in males. Plastral ground color in living specimens pale yellow to orange. 2

2. Head and neck stripes numerous, at posterior edge of tympanum more than 11. C-shaped mark on second pleural scute and/or a dark figure on the plastron. Posterior shell depth (at vertebral III-IV sulcus) 33-36% of carapace length in females and 30-32% in

males. Plastral ground color in living specimens yellow to orange. .... *P. concinna*

Head and neck stripes few, less than 11. No C-shaped mark on second pleural scute and figure absent from plastron. Posterior shell depth (at vertebral III-IV sulcus) 36-38% of carapace length in females and 32-33% in males. Plastral ground color in living specimens pale yellow. .... *P. floridana*

SPECIMENS EXAMINED

Pseudemys rubriventris

New Jersey: MES 132, 1751. North Carolina: MES 1896. NCSM 9360, 16669-70, 16672, 17910, 20116, 20166, 22818, 25080, 28658-59, 28704, 28752-53, 28871, 28897, 28899, 29275-76, 29278, 30034. CM 53026. AMNH 72746, 80218-19, 81869, 90640-44. Pennsylvania: CM 27420, 28969, 29400, 29457, 29502, 31244, 32651. Virginia: AMNH 129302, 129312. CM 13262, 23136. CM(field series) 53632, 53634, 53636, 53695. USNM (field series) 114462, 140441-47, 140759, 157085-88, 157853, 158685, 158881, 159362, 159366, 159568-69, 159572-73. MES 188-90. West Virginia: CM 26630. MES 1902.

Pseudemys concinna

North Carolina: NCSM 6184, 8518, 11364, 11373, 13759, 13810, 13966, 15030, 15135, 17045, 17276, 17339, 17938, 19169, 19356, 19432, 20128, 20236, 20240, 20253, 22966, 24030, 24182, 25044, 25281, 25205-06, 25234, 25265, 26061, 26225, 26525-27, 28688, 29279, 29595, 29968-69, 30038, 30280-81, 30431-34. USNM(field series) 158447. South Carolina: MES 1790, 1875. SREL 2137, 2229. Virginia: USNM(field series) 141102, 141105, 141364, 158811. MES 489. West Virginia: MES 863.

Pseudemys floridana

North Carolina: NCSM 5881, 5883-85, 5927-30, 10330, 11365, 13812-16, 14783, 16476, 17046, 17302, 17581-82, 19353-54, 20190, 20678, 20928, 21001-02, 21603, 23405, 24334, 25737, 25739, 25833, 26344, 26528, 28657, 28705, 28740, 28898, 29301, 29617, 30001, 30291-92, 30423-30. USNM(field series) 158448. South Carolina: AMNH 50985. SREL 0117. Virginia: CM 24447. MES 1900. USNM(field series) 159365.

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